The Effect of Palp Loss on Feeding Behavior of Two Spionid Polychaetes: Changes in Exposure

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Abstract. The effects of sublethal predation on foraging behavior are potentially important. Such predation changes both the condition of the individual and the cost or risk associated with further predation. Tissue loss to predators is a very common phenomenon in marine sedimentary environments; often the tissue lost is the organism's feeding structure. We asked how the loss of feeding structures would affect the foraging behavior of two species of spionid polychaetes, and whether the responses to palp loss are predictable. *Rhyncospio glutaeus* and *Pseudopolydora kempi japonica* represent the ends of a spectrum of risk associated with tissue exposure during feeding. In both species, the loss of one or both palps significantly increased the amount of tissue exposed, and the frequency of exposure, but not the duration of each exposure. All changes were consistent with the normal foraging behaviors of these species. Estimates of relative energy gain suggest that these responses may partially mitigate the effect of palp loss, although potentially increasing the risk of predation.

Introduction

Predation can have profound effects on the foraging behavior of prey organisms, influencing when, where, on what, and how they feed (Lima and Dill, 1990). Trade-offs between food acquisition and risk of predation are common, such as reductions in time spent feeding when predation risk is high (Stein and Magnuson, 1976), use of energetically inferior but secure patches or habitats in the presence of predators (Werner *et al.*, 1983; Gilliam and Fraser, 198 ; Holbrook and Schmitt, 1988), reduced handling time in areas with less cover (Valone and Lima, 1987), and reduced general activity levels in the presence

of predators (Holomuzki and Short, 1988; Main, 1987). Whether animals make such trade-offs can depend on predator abundance, food abundance, the condition of the animal, or a combination of these features (Milinski and Heller, 1978; Mangel and Clark, 1986).

Tissue loss from sublethal predation affects the condition of individuals by changing their physiological state. In addition, such tissue loss may also change the cost or risk associated with further predation [*e.g.,* tailless lizards are more likely to be captured by predators than lizards with intact tails (Dial and Fitzpatrick, 1984; Vitt and Cooper, 1986)]. Sublethal predation is common in marine environments. For example, sediment dwellers (infauna) frequently lose body parts that are exposed above the sediment surface (brittlestar arms: Bowmer and Keegan, 1983; tentacles and tails of worms: De Vlas, 1979a, b; Woodin, 1982; Clavier, 1984; Zajac, 1985; siphons of clams: Edwards and Steele, 1968; Peterson and Quammen, 1982; De Vlas, 1985). Colonial forms living on hard surfaces are often only partially eaten by their predators (Harvell, 1984; Harvell and Suchanek, 1987). Such tissue losses affect growth, reproduction, and activity (growth: De Vlas, 1979b; Peterson and Quammen, 1982; Coen and Heck, 1991; Harvell, 1984; Harvell and Suchanek, 1987; reproduction: Zajac, 1986; Wahle, 1985; activity: Woodin, 1984; Clements, 1985). Moreover, the loss of sensory structures on exposed body parts may impair such organisms' ability to detect predators.

Infaunal animals respond immediately to partial predation by changes in activity and behavior, and thus can be readily used to investigate short term responses to tissue loss. This is particularly true because: (1) the infauna live within a partial predator refuge, the sediment (Virnstein, 1979; Blundon and Kennedy, 1982); (2) their response to predation risk is easily quantifiable as relative exposure outside the sediment; and (3) the tissues lost are often

feeding structures the loss of which directly affects foraging.

Organisms losing feeding structures would appear to have three options representing trade-offs between energetic requirements and risk of further predation: (1) no change in foraging behavior, (2) reduced exposure during foraging, or (3) increased exposure during foraging. Increased exposure might compensate for changes in food intake due to loss of feeding structures but may also increase the risk of further predation. For example, after losing their siphon tips, some bivalves move closer to the sediment surface to maintain their access to the overlying water (Zwarts, 1986). For infauna such as bivalves, predation risk increases as depth in sediment decreases (Blundon and Kennedy, 1982; Zwarts, 1986). Decreased exposure of remaining tissues reduces risk but carries the potential cost of reduced feeding rates and, for bivalves, less access to oxygenated water for respiration. Similarly, infauna that feed on the sediment surface with tentacles or palps may expose more of their body segments following loss of all or part of these feeding structures.

Sih (1987) predicted that animals under increased predation risk should decrease their exposure. In the application of this prediction, predation risk is typically defined by predator abundance, activity levels, and proximity to prey. Use of refuges by prey modifies such predation risk. Similarly, these elements of risk contribute to interactions between sublethal predators and prey (*e.g.,* Levinton, 1971). However, tissue loss may cause physiological and behavioral changes that affect a prey organism's use of refuges. In this study we addressed this modification of refuge use, asking whether, following tissue loss and in the absence of predators, the prey's stereotypical foraging behavior is modified in a way that would change the probability or cost of a second attack. Our goal was to determine how the loss of feeding appendages, a common phenomenon among infauna, would affect tissue exposure in the absence of predators.

For surface-feeding polychaetes such as spionids, feeding incurs risk of tissue loss because it involves exposure of body segments, palps, or both. By removing different amounts of the feeding apparatus (*e.g.,* one *versus* two palps), we could explicitly test whether such tissue losses would result in increased or decreased exposure of body segments. Since infauna escape into the sediment, increased exposure of the body on the sediment surface or shallower burrowing depth are equivalent to increased risk (Blundon and Kennedy, 1982; Zwarts, 1986; Woodin and Merz, 1987). We chose two species that represent extremes of spionid feeding behavior and, given the different feeding behaviors, asked whether the responses to sublethal predation are predictable from a knowledge of normal foraging modes.

Materials and Methods

Study organisms

Rhyncospio glutaeus (Ehlers) and *Pseudopolydora kempi japonica* Imajima and Hartman, are spionid polychaetes common in the intertidal zone of False Bay, San Juan Island, Washington, U. S. A. (48° 29'N: 123° 04'W). *Pseudopolydora* occurs in the high intertidal zone, and *Rhyncospio* in the lower intertidal zone. Both species commonly lose their palps in nature. In 1989 and 1990, 17% of *Rhyncospio* and 8% of *Pseudopolydora* collected from False Bay were regenerating one palp; 10% of *Rhyncospio* and 10% of *Pseudopolydora* collected were regenerating two palps (total collected, n = 466 and 355, respectively). In the absence of high particle flux, both spionid species are surface deposit feeders (Woodin, 1982; Miller and Jumars, 1986). When intact, *Rhyncospio* feeds on the surface by extending both its palps and its body segments (Woodin, 1982), sometimes even feeding directly upon the sediment with its mouth. *Pseudopolydora* rarely extends its body segments, feeding only with its palps on the surface (Woodin, 1982). Both *Rhyncospio* and *Pseudopolydora* have translucent palps, but *Rhyncospio* has about three times as many translucent anterior segments as *Pseudopolydora* (Woodin, 1982). *Rhyncospio* may be up to 15 mm long; *Pseudopolydora* can reach lengths of 30 mm (Wilson, 1984). Worms used in this study were 10 to 15 mm long (*Rhyncospio*), and 15 to 20 mm long (*Pseudopolydora*). The length of the translucent portion of the worms in these size ranges is on average 3.2 mm (15 setigers plus head: *Rhyncospio*) *vs* 1.2 mm (4 setigers plus head: *Pseudopolydora*) (Woodin, 1982; Lindsay, unpubl. data).

Palp removal and behavioral observations

Worms collected from False Bay and transported to the Friday Harbor Laboratories (University of Washington) were stored in sediment cores in a running seawater table. Worms were selected for palp removal within 10 days of collection. Only those with intact, long palps and with no other obvious damage were used. All of the worms selected for observation were relaxed in 1:1 isotonic MgCl$_2$: seawater for 2–3 minutes. There were three treatment groups, worms with 0, 1, or 2 palps removed. The palps were removed at the base where they join the peristomium. *Rhyncospio* palps require a small pull to remove, but *Pseudopolydora* palps drop off easily. After a recovery period (3–5 min) in fresh seawater, the worms were added singly to containers of sieved (0.5 mm mesh) defaunated sediment from False Bay. The mud had been frozen, thawed, rinsed with fresh seawater, placed into containers, and aged in an outdoor seawater tank for 24 h where it developed a surface algal layer. The containers

were 3 cm in diameter, and 9.5 cm deep. After palp removal, worms were allowed a minimum of 24 h to recover from handling before their feeding behavior was recorded on videotape.

Because suspension feeding should be impossible after complete palp loss, this study was restricted to observations of surface deposit feeding behavior, and all observations were made in still seawater. The containers with the worms were submerged in a 1 l beaker of seawater set inside a larger tub of flowing seawater for temperature control. The worms were filmed at night under cool, dark red-filtered fiber optic lights. A video camera attached to a dissecting microscope (at 6×) was suspended above the container. Due to the high resolution of S-VHS videotaping, the palps and segments were both clearly visible against the sediment surface in the low light conditions used for filming.

To limit the range of regenerative states, the worms were placed into their individual containers in groups of nine: three worms per treatment. All nine worms were filmed, and then another group of nine was prepared. All of the worms within a group were typically filmed within 3–4 days of palp removal (in most cases, one worm per treatment per night; *i.e.*, a total of three worms per night). The order in which the worms from each treatment were filmed each night was random. Worms were filmed only if the core surface showed evidence of feeding activity (feces). A total of 36 *Rhyncospio* were filmed: control, n = 11; one palp removed, n = 12; two palps removed, n = 13. A total of 35 *Pseudopolydora* were filmed: control, n = 11; one palp removed, n = 12; two palps removed, n = 12.

Quantifying behavior and statistics

Each worm was videotaped continuously for 2 h, enabling the measurement of true frequencies and durations of behaviors, as well as the times at which feeding behavior patterns stopped and started (Martin and Bateson, 1986). Within the 2 h for a given worm, there were multiple periods during which segments or palps were exposed outside the tube (range: 1 to 68 emergence periods). Each time a worm emerged, we counted the number of segments and palps exposed separately, and the duration of their exposure (seconds). The exposures were considered to have ended when segments or palps withdrew below the tube edge. For clarity of presentation and data analysis, the prostomium and peristomium together were counted as one segment. The prostomium and peristomium are, of course, segmental in the spionids, and are, together, about equivalent to one anterior setiger in both species (Lindsay, *in prep.*). These data were summarized along two time scales, the full 2 h period, and a per emergence scale; thus the frequency, duration and quantity of segment and palp exposure could be described (see Table I).

Table I

Behavioral variables analysed in this study

2-hour time scale
Frequency:
Frequency of segment exposure
Frequency of palp exposures
Duration:
Proportion of 2 h during which any segments were exposed
Proportion of 2 h during which any palps were exposed
Longest duration the maximum number of segments were exposed in 2 h (s)
Quantity:
Mean number of segments exposed in 2 h
Maximum number of segments exposed in 2 h
Per-emergence time scale
Duration:
Duration of segment exposures
Duration of palp exposures
Duration the maximum number of segments were exposed per emergence
Quantity:
Mean number of segments exposed per emergence
Maximum number of segments exposed per emergence

For the 2 h time scale, all variables resulted in one value per worm. For the per emergence time scale, means of the per emergence values for individuals were the data analysed. Potential detectability of a worm by visual predators will increase with increasing frequency or duration of exposure and with increasing amount of tissue (*i.e.*, body segments) exposed.

Variables summarized on a per emergence time scale had distributions within an individual worm, but comparison among all individuals required a single value for each worm. We used the mean of a variable as the value per individual. Although the mode may be a good descriptor of an individual distribution when assessing behavior, it was often not available, did not necessarily occur frequently (a mode could be due to 2 observations out of 25), and was typically equal to or within one standard deviation of the mean of the distribution.

ANOVA was used to determine the effect of palp removal on the behavior variables, with *a posteriori* Bonferroni multiple comparisons among treatment means. When necessary, variables were transformed to meet the assumptions of ANOVA and to correct heteroscedasticity, as noted in Table II (homoscedasticity tested by Scheffé-Box test, Sokal and Rohlf, 1981). All data analysis was done using PC-SAS, version 6.04 (SAS Institute Inc., Cary, North Carolina).

Results

Palp removal had a significant effect on the frequency of segment and palp exposure in *Pseudopolydora;* both increased with palp loss (Table IIA, Figure 1A). The frequency of segment and palp exposure did not change significantly with palp loss in *Rhyncospio* (Table IIA).

Table II

Effect of palp removal on spionid feeding behavior variables

Behavior variable	Rhyncospio Treatment mean					Pseudopolydora Treatment mean				
	0	1	2	F	sig	0	1	2	F	sig
A. *2-hour time scale*										
a,b Frequency of segment exposure	16.69	21.71	15.17	0.89	ns	2.28	4.60	7.72	2.95	*
Mean number of segments exposed in 2 h	3.70	4.45	5.32	3.24	*	1.14	1.13	1.56	1.91	ns
Maximum number segments exposed in 2 h	10.09	11.83	12.23	0.62	ns	1.73	1.83	3.25	4.54	**
a,c Longest duration maximum number segments out in 2 h (s)	11.32	9.08	12.77	0.28	ns	32.67	51.14	44.99	0.67	ns
a,b Proportion of 2 h that segments were exposed	0.05	0.09	0.07	0.59	ns	0.002	0.004	0.01	2.46	ns
Frequency of palp exposure	24.64	20.67	NA	1.44	ns	14.27	19.17	NA	7.08	**
Proportion of 2 h that palps were exposed	0.27	0.35	NA	1.07	ns	0.83	0.90	NA	0.84	ns
B. *Per-emergence time scale*										
a,d Mean number segments out per emergence	3.12	3.56	4.84	7.02	****	1.09	1.07	1.44	1.59	ns
a,d Maximum number segments out per emergence	3.72	4.41	6.52	8.01	****	1.21	1.12	1.73	2.77	*
a,b,d Duration maximum number segments out per emergence (s)	12.73	10.98	13.64	0.67	ns	2.98	4.73	4.38	0.47	ns
b,d Mean duration segment exposures (s)	24.26	26.46	32.30	0.93	ns	4.39	5.57	7.24	0.50	ns
a,d Mean duration palp exposures (s)	77.16	110.9	NA	1.96	ns	435.3	370.8	NA	0.35	ns

[a] *Rhyncospio:* Variable was square-root transformed in analysis; back-transformed means given.

[b] *Pseudopolydora:* Variable was square-root transformed in analysis; back-transformed means given.

[c] *Pseudopolydora:* Variable was log $(x + 1)$ transformed in analysis; back-transformed means given.

[d] Variable has a distribution across an individual. Means of per emergence values were used in the analysis; both species.

Results of one-way ANOVA with palp removal as the main effect. Palp removal treatments are 0, 1, or 2 palps removed. When variables were transformed to meet assumptions of ANOVA, back-transformed treatment means are given. Results of Bonferroni multiple comparisons are given in the figure or text for variables with F values significant at $P \leq 0.05$. Probability of significance is indicated as follows: *: $P < 0.10$, **: $P \leq 0.05$, ***: $P \leq 0.01$, ****: $P \leq 0.005$, n.s.: not significant, NA: not applicable.

The total proportion of time that any segments were exposed over the 2 h observation period was low for both species and did not change significantly with palp loss (Table IIA). Similarly, palp loss did not significantly affect the total time palps were exposed in either species (Table IIA). Neither the mean duration of segment exposures nor the mean duration of palp exposures changed significantly with palp loss in either *Rhyncospio* or *Pseudopolydora* (Table IIB). Another duration variable of interest, in terms of exposure outside the sediment refuge, is the amount of time the maximum amount of tissue is exposed by a worm. The longest duration that the greatest number of segments were exposed in 2 h showed no significant difference with palp loss for either *Rhyncospio* or *Pseudopolydora* (Table IIA). Similarly, palp loss had no effect on the length of time that the maximum number of segments were exposed per emergence in either species (Table IIB).

Measures of the quantity of segment exposure increased significantly with palp removal in both *Rhyncospio* and *Pseudopolydora* (Table II). The mean number of segments that were exposed in a 2 h period increased from 3.7 (control average) to 5.3 segments for *Rhyncospio* with no palps

(two palps removed) (Table IIA, Fig. 1B). Intact *Pseudopolydora* on average extended only one segment, and this did not change significantly with palp removal. The maximum number of segments exposed in the 2 h period represents the furthest degree to which a worm exposed its body during the period. *Pseudopolydora* with two palps removed extended significantly more segments at maximum in the 2 h than intact worms, although the increase was small, from 1.7 to 3.2 segments (Table IIA, Bonferroni multiple comparison test, $\alpha = 0.05$). Over a 2 h period, *Rhyncospio* exposed at maximum 10 to 12 segments, showing no significant response to palp removal (Table IIA).

Rhyncospio with no palps (two palps removed) extended significantly more segments at maximum per emergence than those with one or two palps (Fig. 1C, Table IIB). In fact, the difference between an average of 3.7 (control) and 6.5 segments (two palps removed) exposed represents an 80% increase in the average maximum amount of tissue exposed by the worms per emergence. While the maximum number of segments exposed per emergence was statistically greater than controls for *Pseudopolydora* with no palps (Table IIB), the difference be-
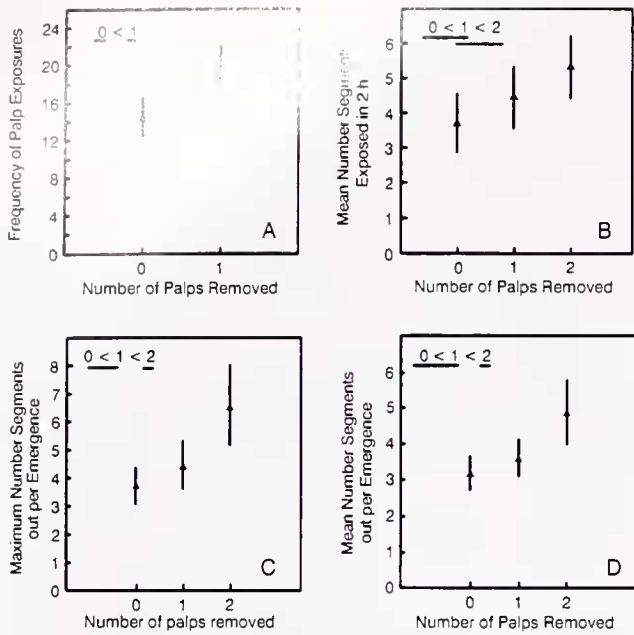
Figure 1. The effect of palp removal on tissue exposure by *Rhyncospio* and *Pseudopolydora* (means and 95% C.I.). Inequalities indicate the results of Bonferroni multiple comparisons among means. Treatments underlined by the same line are not significantly different at an $\alpha = 0.05$ experimentwise error rate. (A) Frequency of palp exposure, *Pseudopolydora;* (B) Mean number of segments exposed in 2 h, *Rhyncospio;* (C) Maximum number of segments out per emergence, *Rhyncospio;* (D) Mean number of segments out per emergence, *Rhyncospio.* In (C) and (D) back-transformed means and 95% C.I.s are plotted; Bonferroni results are for comparisons made among transformed means used in the ANOVA.

tween 1.2 (control) and 1.7 segments (two palps removed) is quite small.

The mean number of segments worms exposed per emergence is consistent with the mean number of segments exposed in the 2 h period. *Pseudopolydora* with no palps (two palps removed) tended to expose more segments per emergence than those with one or two palps, but the change is very small and not significant (Table IIB). *Rhyncospio* with no palps exposed significantly more segments per emergence than those with one or two palps (Fig. 1D and Table IIB).

Because both spionid species have anterior body segments that are relatively translucent and presumably cryptic (Woodin, 1982), increases in the quantity of segment exposure are also considered with respect to the coloration of the tissue exposed. Both *Rhyncospio* and *Pseudopolydora* increased the quantity of segment exposure in response to palp loss (Table II). But the maximum number of segments exposed per emergence by *Rhyncospio* (6.5 ± 2.2, X ± S.D., n = 13) (Fig. 1C) is well within the range of translucent anterior segments reported by Woodin (1982): 15.1 ± 3.2 (X ± S.D., n = 42). In fact,

the maximum number of segments exposed in the 2 h by *Rhyncospio* with no palps, 12.2 ± 4.4 (X ± S.D., n = 13), is also within the range of translucent segments. The same is true for *Pseudopolydora.* The maximum number of segments exposed in 2 h by individuals with no palps, 3.2 ± 1.5 (X ± S.D., n = 12) (Table IIA), is within the range of translucent anterior segments reported by Woodin (1982): 4.3 ± 3.7 (X ± S.D., n = 51).

The normal feeding behavior of *Rhyncospio* would appear to involve more risk than that of *Pseudopolydora:* exposure of more segments (and more metric length: 0.74 mm *vs.* 0.27 mm) with greater frequency and duration (controls, Table II), as well as longer periods of exposure to aquatic predators, because *Rhyncospio* lives in the lower intertidal zone. The occurrence of worms in the field regenerating one palp seems to support this; twice as many *Rhyncospio* as *Pseudopolydora* were found regenerating one palp (17%: n = 466 and 8%: n = 355, respectively; these proportions are significantly different, z-test, z = 3.83, $P \leq 0.05$). However, the percentage of worms regenerating two palps was the same for both species: 10%. The translucence of the anterior tissues (*i.e.,* crypsis) probably decreases detectability of spionids by visual predators, but does not render them invisible. Following palp loss, all increases in body segment exposure were within the translucent portions of the worms.

Discussion

For prey, risk is a measure of exposure determined by predator access, abundance, and activity, as well as by the behavior of prey. In these experiments, we measured changes in refuge use by infaunal prey (spionid polychaetes) following tissue loss. Because the sediment acts as a partial refuge from predation for infauna (Virnstein, 1979; Blundon and Kennedy, 1982), any increase in exposure on the sediment surface represents increased risk in the same sense that emergences from other refuges, such as crevices and complex structures, represent increased risk (fish: Sale, 1971; brittlestars: Sides, 1981; harpacticoid copepods: Coull and Wells, 1983). Thus, in our experiments we equated risk with increases in emergence of spionids onto the sediment surface following tissue loss. These experiments were conducted in the absence of predators or competitors. Clearly, the presence of either of these may affect the behavior of the spionids. In the presence of predators or competitors we would expect a reduction in the differences in exposure between worms with palps and worms with no palps due mainly to decreased activity of all worms. This expectation is based upon numerous observations that infauna (particularly spionids) withdraw into the sediment with changes in light intensity, shadowing, vibration, water pressure, physical contact with tubes or body parts etc., all of which are

presumably associated with predators (*e.g.*, fish and shrimp), competitors (*e.g.*, other spionids), or even with physical events which could cause damage to the animal. Our results, then, represent a baseline description of the effect of tissue loss on behavior and refuge use.

Increased exposure with tissue loss

Juvenile flatfish, such as plaice and dab, are well-known partial predators, with bivalve siphons and polychaete tentacles constituting the majority of their diets (Edwards and Steele, 1968; De Vlas, 1979a). These predators scan the sediment surface for prey and pounce upon it; dab in particular rely on visual cues, whereas plaice also employ chemical detection of prey (De Groot, 1971). Given such predators, the frequency, duration, and quantity of tissue exposure directly contribute to prey detectability. By simple chance, more frequent exposure increases the chance of detection. Similarly, a predator will have more time to identify prey as the duration of prey exposure increases. The quantity of its tissue exposed will also contribute to prey detectability.

For both *Rhyncospio* and *Pseudopolydora*, feeding behaviors following palp loss were expansions of their normal feeding behaviors, with no radical alterations; thus intact feeding behaviors may be useful for predicting the behavioral response of spionid polychaetes to palp loss. *Rhyncospio* often exposes segments during feeding, while *Pseudopolydora* does not (controls, Table II). Loss of feeding structures in *Rhyncospio* resulted in much greater exposure of segments than in *Pseudopolydora* (Table IIB). *Pseudopolydora* feeds primarily with its palps, and following loss of one palp, frequency of exposure of the remaining palp increased. Tissue loss caused increased exposure of anterior tissues in both species (Table II), and this increased exposure should be associated with increased risk.

Trade-offs of risk and energy?

The behavioral options for foraging animals lie on a continuum between energy maximization (at the expense of predator avoidance) and risk minimization (at the expense of feeding). Loss of feeding structures might constrain infauna to feed at, or closer to, either of these extremes. For instance, spionids with no palps may either expose body segments to feed upon the surface with their mouths (at the expense of increased chance of detection by predators), or these worms may not feed at all, remaining within the sediment refuge.

We observed increased tissue exposure following palp loss in both species of spionids examined. Assuming that all exposure is associated with feeding, the advantage of continued feeding might contribute to the observed increase in exposure. The worms probably did not face starvation, as evidenced by the presence of feces on cores within 2 to 5 days after removal of two palps from worms of both species. Nevertheless, continued and increased exposure for feeding may speed palp regeneration, thereby minimizing the impact of palp loss. Do the observed increases in exposure result in increased energy gain? Although we did not measure growth in these experiments, by relating the time spent feeding to intake rate and hence energy gain, we can make some estimates of the energy gain associated with the responses of these polychaetes.

Assuming no changes in the efficiency of digestion and assimilation following palp loss, energy gain will be directly related to intake rate. If we assume that a worm with one palp feeds with 50% of the collection efficiency of an intact worm and that time spent feeding is proportional to energy intake, then we can use our data on palp and segment exposure times to estimate relative energy gain per treatment by the following calculations: for the control, (time that the two palps are exposed × 1); for worms with one palp, (time that the palp is exposed × 0.5); with no palps, (time that the segments are exposed). Exposure times are calculated by multiplying the frequency of exposure by the duration of exposure, using appropriate treatment means from Table II. Note that, in over 99% of the cases, when the segments are exposed, the palps are exposed; thus only in the no palp treatment must we use segment exposure times in the calculations. For these calculations, we have assumed that all exposure is associated with feeding. For *Rhyncospio*, at least, this is probably not true and further study may reveal shifts in the time spent feeding following palp loss.

By the above calculation, loss of one palp by *Rhyncospio* would reduce the worm's relative energy intake by 40%, and loss of both palps would result in a 74% reduction relative to controls. For *Pseudopolydora*, the reductions are even more dramatic: 43% and 99%. Note that, for both species, the relative reduction in energy gain following the loss of one palp is less than the 50% that would be expected if there were no changes in exposure.

Woodin's (1984) data on weights of feces of another spionid, *Spiophanes bombyx*, following palp loss suggest no change in efficiency following the loss of one palp, but reduced efficiency following the loss of two palps. Changing our calculations to time exposed, with no adjustment for one or two palps present, we find no significant change between controls and one palp treatments for *Rhyncospio* (*i.e.*, no difference in palp exposure times, Table II) but still a 74% reduction for the no palp treatment. *Rhyncospio* is similar to *Spiophanes* in its feeding mode, and this pattern of reduction is similar as well. Woodin (1984) saw no reduction in fecal weights of *Spiophanes* with one palp, but observed a 35% reduction in fecal weights of those with no palps. For *Pseudopolydora*, assuming no change in efficiency following the loss of one palp, relative energy

intake would increase 14% for the one palp treatment relative to controls (due to the significant increase in palp exposure in the one palp treatment) and would be reduced by 99% for the no palp treatment.

From both calculations, loss of both palps, a common phenomenon for numerous species including *Rhyncospio* and *Pseudopolydora*, has striking effects on relative energy gain. These calculations also show that increased palp exposure by *Pseudopolydora* with one palp ablated resulted in an apparent increase in relative energy gain. But, because *Pseudopolydora* did not change its segment exposure after losing both palps, as predicted by normal foraging behavior, it incurred a 99% reduction in relative energy intake. Normal feeding behavior in *Rhyncospio* involves segment exposure and, after the loss of two palps, the amount of segment exposure increased (Table II). But, to compensate for the loss of both palps, the frequency and duration of segment exposure would have to increase, and they did not (Table II), resulting in a 74% reduction in relative energy intake. Whether the changes in frequency, duration, and quantity of tissue exposure are a reflection of the relative risk of these three behaviors awaits further study.

Another factor that might contribute to energy gain is the area of sediment surface to which a worm may have access. This feeding area is directly determined by the amount of tissue exposed, which as we have shown, increased with palp loss. We describe the feeding area available to a worm as circular, with the tube opening at the center. The radius of this circle is determined by the average length of tissue exposed, which is the sum of segment and palp lengths. Segment length is equivalent to the product of the length per anterior segment (*Rhyncospio*: 0.2 mm; *Pseudopolydora*: 0.24 mm) and the average number of segments exposed in 2 h (Table IIA, treatment means). Palp length is the average palp length of worms in the appropriate treatment (*Rhyncospio* controls: 2.7 mm; *Pseudopolydora* controls: 10.2 mm).

By this calculation, the feeding area of intact *Rhyncospio* is 37.0 mm². Following palp loss, the feeding radius is determined by the length of body segments exposed. For *Rhyncospio* with no palps, the feeding area is 3.5 mm². For *Rhyncospio* in this study, loss of two palps resulted in a 90% reduction of the average area accessible for feeding.

Intact *Pseudopolydora* have longer palps than intact *Rhyncospio*, therefore, a longer feeding radius as well. For intact *Pseudopolydora* in this study, the feeding area is 344.0 mm². Because *Pseudopolydora* with no palps extended very few segments, their potential feeding area was drastically reduced. The feeding area of *Pseudopolydora* with no palps is 0.4 min²!

Like the relative energy gain calculations, these suggest that palp loss will dramatically reduce the accessible feeding area for these worms. Although *Rhyncospio* with no palps significantly increased its exposure of segments (Table II), this increase was not enough to compensate for the loss of palps. The feeding area of *Pseudopolydora* with no palps was even more drastically reduced. In terms of energy gain, the relative importance of these changes in feeding area following palp loss will be modified by the hydrodynamic regime of the worms' habitat and by particle re-supply rates. High particle re-supply rates may mitigate the effect of a reduced feeding area (Miller *et al.*, 1984).

These results emphasize the need to consider the foraging behavior of infauna with respect to the effects of partial predation, particularly because infauna often lose feeding structures. Like lethal predation risk, partial predation can influence when (Levinton, 1971) and where (this paper) infauna feed. For spionids losing palps, the potential advantage to continued feeding and therefore faster palp regeneration may cause increases in the exposure of the remaining tissues (Table II, Fig. 1). These increases in exposure may mitigate the effect of palp loss on relative energy intake but may also increase risk. Given the demonstrated changes in feeding behavior following palp loss in spionid polychaetes and the potential increase in risk associated with increased tissue exposure, consideration of the regenerative state of the animal and consequent changes in behavior is especially important in foraging models of infauna.

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